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NEW ECHIMYID RODENTS FROM THE OLIGOCENE OF PATAGONIA, AND A SYNOPSIS OF THE FAMILY

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ABSTRACT. The living and extinct echimyid rodents are briefly reviewed, and placed in five subfamilies: Echimyinae Murray, Dactylomyinae Tate, Heteropsomyinae Anthony, Myocastorinae Ameghino, and Adelphomyinae nov. *Prospaniomys* and *Spaniomys* are placed in the Myocastorinae. Two new genera and species, *Xylechimys obliquus*, Deseadan, and *Paradelphomys fissus*, Colhuehuapian, are described; both are referred to the Adelphomyinae.

A SYNOPSIS OF THE ECHIMYIDAE

Echimyids today form the largest of the numerous families comprising the suborder Caviomorpha. Fifteen living genera are currently recognized, all but one wholly tropical or subtropical in distribution. Extinct genera, including those described below, number only eighteen and of these four are Antillean. We are hence far from a really adequate understanding of the phylogeny of the group. The living forms have usually been divided into two subfamilies, Dactylomyinae and Echimyinae (e.g. Ellerman, 1940;²

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² Ellerman, while recognizing these subfamilies, also included in his Echimyidae, with the rank of subfamily, the Octodontidae (with *Ctenomys*), Abrocomidae, Capromyidae, *Plagiodontia*, *Myocastor* and even the African Thryonomyidae and Petromuridae. As will appear below, we agree as to recognition and inclusion of the Myocastorinae. Further work may require that the brachyodont to hypsodont Echimyidae and the hypselodont Capromyidae be merged; in that case the subfamilies of each would become tribes. The octodontids surely had a common origin with the echimyids in pre-Deseadan time, but the two groups diverged thereafter and merit familial rank. Abrocomids and ctenomyids are derivatives of the Octodontidae, the *Ctenomys* group being only a subfamily of it. The African families have nothing to do with this assemblage, being descended from the Fayum Phiomyidae (Lavocat, 1963; Wood, in press).

Cabrera, 1960), with the extinct forms placed in the latter (e.g. Simpson, 1945). There can be little doubt that *Dactylomys* and its relatives constitute a single suprageneric group, but the same can hardly be claimed for the Echimyinae, particularly if the extinct forms are taken into account. Wood and Patterson (1959:301-2), on the basis of work in manuscript by Patterson and Kraglievich, divided the family into five groups: the *Proechimys-Eumysops*, the *Dactylomys*, the *Echimys*, the *Spaniomys* and the *Adelphomys*. The *Echimys* and *Dactylomys* groups are so far unrepresented, or at least unrecognized, in the fossil record. The largest group and the one with the most continuous record is the *Proechimys-Eumysops*, which can be traced back to the Colhuehuapian Oligocene *Protacaremys*; it includes almost half of the known genera. The *Echimys* group, the Echimyinae proper, comprises only three genera. Ellerman (1940:106-108) pointed out the distinctions between these three and the rest of his Echimyinae but did not separate them formally. The extinct West Indian *Heteropsomys*, *Homopsomys*, *Brotomys* and *Boromys* appear to be closer to the *Proechimys-Eumysops* group than to any other division of the family (Miller, 1930; Williams and Koopman, 1951), and Kraglievich (1957, 1965) has extended Anthony's subfamily Heteropsomyinae¹ (1917) to include the whole assemblage. As regards two other extinct Antillean genera, *Isolobodon* and *Aphaetreus*, that are often placed in the Echimyidae, we are inclined for the present to follow Miller and Kellogg (1955:644-5) and associate them with *Plagiodontia* as a subfamily of the Capromyidae.

Wood and Patterson placed *Spaniomys* and *Prospaniomys* in a separate group on the basis of cheek tooth structure, but did not comment as to possible relationships to later forms. We now offer the suggestion that *Myocastor* may be a survivor of this group. This rather specialized genus does not fit comfortably into the Capromyidae — otherwise a purely Antillean group so far as known² — with which it is frequently associated. It also stands somewhat apart from the later Echimyidae in such characters as the very long paroccipital process, the prominent lateral process of the supraoccipital, the greatly reduced coronoid process, the presence of four fully developed lophids in all lower molars and five

¹ Proposed by Anthony on the supposition that he was defining a subfamily of the Dasyproctidae. This is the oldest available name, antedating Eumysopidae Rusconi 1935 (Eumysopinae Kraglievich 1945).

² The Venezuelan record of "*Procapromys*" was surely based on erroneous locality data.

lophids and a small anterior fossettid in dm_4 . A tendency toward reduction and loss of the metalophid in the molars is characteristic of the family. Dactylomyines, echimyines and most later members of the *Adelphomys* group (see below) lack it, while heteropomyines may retain a vestige of it, or, alternatively, acquire a neolophid, on anterior lower molars, in the form of a small crest, connecting anterolophid and hypolophid, that isolates a small anterointernal fossettid. The members of the *Spaniomys* group do not display this tendency to the same degree. In the Colhuehuapian *Prospaniomys* the metalophid is present in M_{1-2} and interrupted or absent in M_3 ; in the Santacruzian *Spaniomys* it is present in M_{1-2} and absent in M_3 . The cheek teeth of *Spaniomys* are quite variable, however, and two specimens in the Ameghino Collection display a tendency toward reacquisition of a fourth lophid in M_3 . In one of these there is a pronounced spur projecting posteriorly from near the center of the hypolophid, and in the other (the type of *Graphimys provectus* Ameghino, a synonym of *Spaniomys modestus* Ameghino) this spur is larger, extending to the posterointernal corner of the tooth. The end result of this, if continued, would have been an M_3 with four lophids, the third of which, while resembling the third (the metalophid) of M_{1-2} , would have been a neomorph.

Unworn and, especially, little worn upper and lower molars of *Myocastor* (there is much change in crown proportions and some in structure as wear proceeds) resemble the corresponding teeth of *Prospaniomys* and *Spaniomys* more closely than they do those of other echimyids. The fourth crest of M_3 could have been inherited either from ancestors like *Prospaniomys*, in which the crest was still present in certain individuals, even if somewhat reduced, or from ancestors resembling *Spaniomys*, in which the tendency toward a neomorph crest had become fixed. Dm^4 of *Myocastor* is fully molariform as is that of *Prospaniomys*; *Spaniomys* differs in having only three lophids. Dm_4 of *Myocastor* is a complex tooth with five lophids, the anterior two united lingually to isolate the small anterior fossettid. *Spaniomys* has four lophids, the anterior pair uniting lingually with wear to isolate one or two shallow fossettids; in *Prospaniomys* the two anterior lophids are united at or shortly following eruption. These crests correspond topographically to the anterolophid and metalophid of the molars. The small extra lophid of *Myocastor* (the second in the series) is an addition to the crown. Acquisition of this crest by the ancestors of the living form seems likely. In one species of the late Pliocene *Isomyopotamus* the rather large anterior fossettid is partially

divided by a spur directed internally from the united anterolophid and metalophid (Reig, 1950:113, fig. 2c); this suggests a method of origin of the extra lophid. *Myocastor* is specialized as regards the progressive enlargement of the cheek teeth from dm_4 backward and the progressive obliquity of the lophids in the lower series. In the late Pliocene *Isomyopotamus* and *Paramyocastor* (Ameghino, 1904:252) these tendencies are less marked.

An imperfect skull of *Spaniomyis* is known (Scott, 1905:410-411). This displays certain resemblances to *Myocastor*. The rostrum is relatively long and its ventral border somewhat elevated above the bony palate, the tip of the upper incisor is approximately at the level of the cheek teeth, the paroccipital processes are longer and the lateral processes are freely projecting (*vide* Scott¹). The coronoid process of the mandible is not reduced, but such reduction may have been a late event in the group. Ameghino describes the coronoid of *Paramyocastor* as being "mucho más larga que en

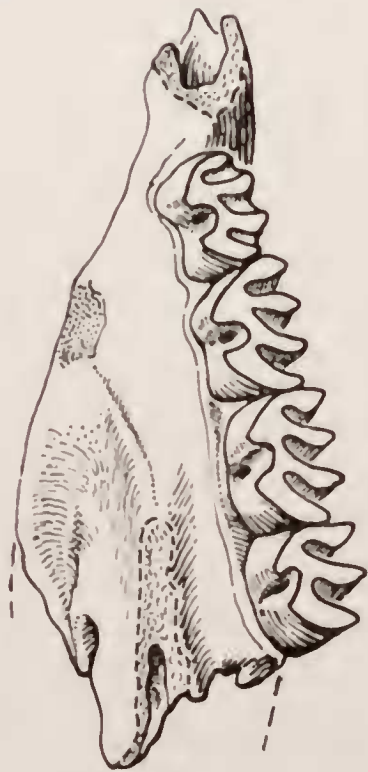


Fig. 1. *Spaniomyis modestus* Ameghino. $\times 4$. Princeton University No. 15577. Dorsal view of incomplete left mandible.

¹ The specimen (American Museum No. 9529) does not now show these last two features clearly; possibly it has suffered some damage since 1905.

Myocastor." *Myocastor* has a very large, wide masseteric shelf that begins beneath M_1 and runs back to the angle. *Spaniomys* possesses a smaller but nevertheless rather comparable structure so far as preserved (Fig. 1). Both forms have a muscle scar running from the coronoid process to the front of the shelf; and in both the grinding surface of the upper cheek teeth faces somewhat outwardly, that of the lowers inwardly.

These resemblances in skull and dentition are collectively rather impressive. We believe a relationship to be possible and accordingly for the present include the *Spaniomys* group in the *Myocastorinae*. The test of this hypothesis will come with the discovery of late Miocene and earlier Pliocene forms ancestral to the later Pliocene myocastorines *Isomyopotamus* and *Paramyocastor*.

The *Adelphomys* group remains for consideration. It was the earliest of the several subdivisions to appear in the record and is the only one that, so far as can be judged on present evidence, has no surviving representatives. *Deseadomys* (Wood and Patterson, 1959:303-312) and *Xylechimys* gen. nov. of the early Oligocene are higher crowned than the late Oligocene *Protacaremys* and *Prospaniomys*, and are more advanced as regards obliquity of lophs and lophids and (in *Deseadomys*) reduction or loss of the metalophid in the lower molars. *Deseadomys* and *Xylechimys* differ from all later echimyids in the replacement of dm_4^+ by P_4^+ . As pointed out by Wood and Patterson (1959:301), retention of the milk molars in the family presumably came about between Deseadan and Colhuehuapian time. There appears to have been an early dichotomy into the *Adelphomys* group, on one hand, and the ancestors of the rest of the family, on the other (Wood and Patterson, 1959, fig. 3), and it follows from this that retention of dm_4^+ has occurred more than once in echimyid history.¹ The group is distinct from the time of its earliest appearance, survived into the early Pliocene, and includes a third of the extinct genera. It is worthy of subfamilial rank and may be defined as follows:

ADELPHOMYINAE subfam. nov. Cheek teeth sub-mesodont to mesodont, no unilateral hypsodonty; lophs and lophids tending to become markedly oblique, sometimes lamellar; upper molars with metaloph and posteroloph uniting early to convert metaflexus

¹ The selective advantage of retention of dm_4^+ , especially in groups that retained brachyodont teeth throughout their subsequent history, is not too clear. A possible explanation might be that this afforded a simpler, more rapid means of attaining crown complexity than progressive molarization of P_4^+ , dm_4^+ being of course more complex than the replacing tooth.

to metafossette, other flexi persistent; lower molars with marked tendency toward reduction and loss of metalophid.

Distribution: Early Oligocene to early Pliocene, South America.

Genera: *Adelphomys*, *Stichomys*, Santacruzian; *Paradelphomys* gen. nov., Colhuehuapian; *Xylechimys* gen. nov., *Deseadomys*, Deseadan. There is, in addition, an undescribed genus in the Chasican (Pascual, MS).

The distinctive characters of the cheek teeth of the other subfamilies may be summarized, with a listing of the included genera:

Echimyinae Murray 1866.¹ Mesodont, relatively long; lophs and lophids rather stout, tending to form transverse lamellae; flexi and flexids (or transverse valleys) fairly persistent. *Echimys*, *Diplomys*, Central and South America, *Isothrix*, South America, Recent.

Dactylomyinae Tate 1935. Brachyodont, wide, large relative to size of skull; lophs and lophids rather thin, sharp and with tendencies toward acquisition of lamellae; flexi and flexids persistent. *Dactylomys*, *Thrinacodus*, *Kannabateomys*, South America, Recent.

Heteropsomyinae Anthony 1917. Brachyodont to hypsodont, with some unilateral hypsodonty; upper cheek teeth tending to become subcircular to quadrate in outline; flexi and flexids not very persistent, converting to fossettes and fossettids after moderate wear; small anterointernal fossettoid may be present in lower molars. *Proëchimys*, Central and South America, Recent, Puerto Rico, uncertain age; *Hoplomys*, Central and South America, Recent; *Euryzygomatomys*, *Clyomys*, *Mesomys*, *Lonchothrix*, South America, Recent; *Carterodon*, South America, Pleistocene to Recent; *Cercomys*, South America, Pliocene to Recent; *Heteropsomys*, *Homopsomys*, Puerto Rico, latest Pleistocene or early Recent; *Brotomys*, Hispaniola, latest Pleistocene or early Recent; *Boromys*, Cuba, latest Pleistocene or early Recent; *Eumysops*, South America, late Pliocene to Pleistocene; *Protacaremys*, South America, late Oligocene. *Protadelphomys*, South America, late Oligocene, is tentatively placed here, and there is an undescribed genus in the Santa Cruz Miocene of Patagonia.

Myocastorinae Ameghino 1904.² Brachyodont to hypsodont; labial flexi and lingual flexids of later forms converting to fossettes and fossettids after considerable wear; later forms showing an increase in size and in obliquity of lophs and lophids from front to

¹ As Echimyina (= Echymyna Gray 1825, Echymidae Bonaparte 1845).

² Proposed as a family (= Myopotamini Tullberg 1900, Myiopotamyina Bonaparte 1850).

back; dm_4 with a small anterior fossettid, with five lophids in later forms; M_3 usually with four lophids, metalophid either retained or a third lophid reacquired. *Myocastor*, South America, Pliocene?, Pleistocene to Recent (and currently doing only too well in the feral state in Europe and North America); *Paramyocastor*, *Iso-myopotamus*, South America, late Pliocene; *Spaniomys*, South America, early Miocene; *Prospaniomys*, South America, late Oligocene. *Tramyocastor* does not appear to be separable from *Myocastor*.

The new genera to be described, one of them Deseadan, the other Colhuehuapian, are both adelphomyines and appear to be more closely related to each other than to any of the previously known forms.

DESCRIPTION OF NEW FORMS

XYLECHIMYS¹ gen. nov.

*Type species: X. obliquus*¹ sp. nov.

Distribution: Deseadan, Patagonia.

Diagnosis: Reduced metalophid present on all molars, joined to metaconid to isolate antero-fossettid but continuing on into mesoflexid to define small anteroflexid, metalophid smallest in M_3 , subequal in M_{1-2} ; hypolophid and posterolophid very oblique, especially on M_{1-2} ; posterolophid terminating linguallly near median line of tooth row; principal flexids deep, all of nearly equal depth on M_{2-3} , metaflexid shallower on M_1 ; metaconid sharply angulate posteriorly.

XYLECHIMYS OBLIQUUS sp. nov.

Type: Museo de La Plata No. 59. II. 26. 81, portion of right ramus with M_{1-3} , base of I and alveoli of P_4 .

Hypodigm: Type only.

Horizon and locality: Deseadan Oligocene; Laguna de los Machos, Campo Belisario Escobar, Departamento Paso de los Indios, Chubut, Argentina.²

Diagnosis: As for the genus.

¹ ξύλον, wood, plus *Echimy*s. Named for Professor Albert E. Wood in recognition of his contributions to our knowledge of the order. The specific name refers to the obliquity of the posterior lophids.

² This is a new locality that has yielded a small faunule. Found with *Xylechimys* were specimens of *Asteromys*, *Archaeohyrax*, *Plagiarthrus*, *Pro-pachyrucos*, *Prohegetotherium*, Trachytheriinae indet., which are sufficient to reveal the age.

Description: The anterior cheek tooth is unfortunately represented only by its broken alveoli. X-rays reveal no trace of a tooth below these alveoli. It is virtually certain that the missing tooth was P_4 , as in *Deseadomys*.

The molars are mesodont and exhibit no tendency toward unilateral hypsodonty. M_2 is the largest, and M_3 the smallest of the series, but the size differences are not great. All are broader relative to length than in *Deseadomys* and are wider anteriorly than posteriorly, most notably as regards M_3 . The anterior portions of the molars are short anteroposteriorly.

The anterolophids are nearly transverse. A reduced metalophid is present on all teeth, that of M_3 being the shortest, those of M_{1-2} subequal. Near the middle of its course each metalophid is united to the metaconid to isolate a small anterofossettid, and then continues lingually beyond this junction for a short distance. A short



A



B

Fig. 2. *Xylechimys obliquus* gen. et sp. nov. $\times 10$. Type. Museo de La Plata No. 59. II. 26. 81. A, RM_{1-3} , crown view; B, RM_{1-3} , lingual view.

and shallow anteroflexid is thus present in addition to the anterofossettid, a marked contrast to *Deseadomys arambourgi*. The hypolophid is decidedly oblique, being almost in a direct line with the ectolophid. On M_{1-2} , but not on M_3 , this crest is slightly swollen lingually, the swelling marking the position of the entoconid. The posterolophid is essentially parallel to the hypolophid and terminates posteriorly a short distance lingual to the mid-line of each tooth. The metaconid is sharply angulate posteriorly. Hypoflexid and mesoflexid are of equal depth, extending nearly to the base of the enamel. The metaflexid progressively deepens posteriorly through the series until it is as deep as the hypoflexid and mesoflexid on M_3 . The walls of these three valleys are steep. In M_{2-3} , especially in the latter, these flexids deepen toward the mid-line. The anterofossettid is shallower than the principal flexids, and the anteroflexid is little more than a conspicuous groove. The mesoflexid and anteroflexid together constitute the largest valley in M_{1-2} . On M_3 the connection between the posterolophid and the ectolophid had not yet been fully established by wear, which suggests that in the unworn state a gap existed between these lophids. On M_3 a slight notch in the anterior wall of the anterofossettid had not yet been obliterated by wear.

The base of the incisor is poorly preserved. All that can be said concerning it is that the enamel extends about half way around the lateral face.

The mandibular ramus, so far as preserved, is robust and deep, about as in *Deseadomys*. As in that form, the ascending ramus arises near the front of M_3 . The masseteric crest begins, as a small shelf, at a point beneath the anterior portion of M_1 .

PARADELPHOMYS¹ gen. nov.

*Type species: Paradelphomys fissus*¹ sp. nov.

Distribution: Colhuehuapian, Oligocene, Patagonia.

Diagnosis: Lophids very oblique, posterolophid forming an isolated lamella; metalophid vestigial on dm_4 , absent on molars; anterofossettid of dm_4 elongate.

PARADELPHOMYS FISSUS sp. nov.

Type: Museo municipal de Mar del Plata No. 125, fragment of right mandible with dm_4 — M_1 .

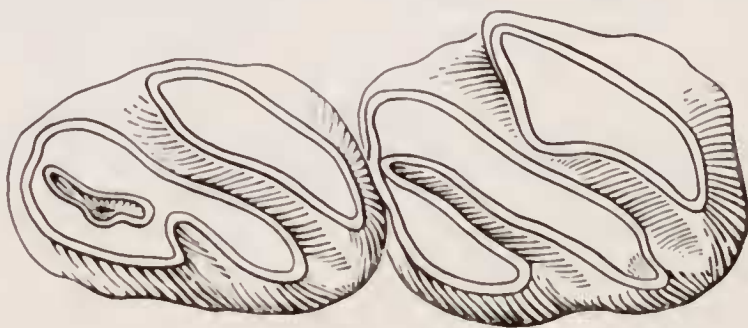
¹ *para*, beside, plus *Adelphomys*. The specific name alludes to the isolation of the posterolophid.

Hypodigm: Type only.

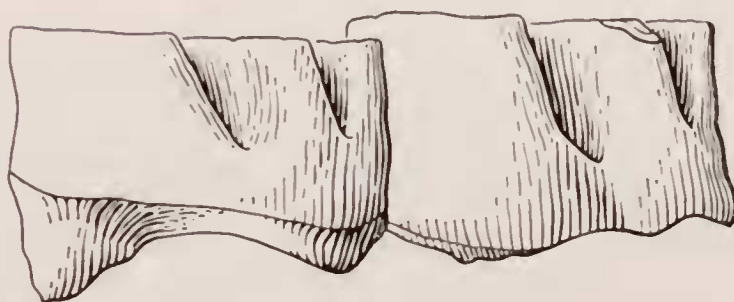
Horizon and locality: Colhué-Huapí Formation; barranca south of Lake Colhué-Huapí, Chubut, Argentina.

Diagnosis: As for the genus.

Description: Dm_1 is nearly oval in outline and longer than M_1 . The anterolophid is gently convex anteriorly and very obliquely directed posterolingually. Near its extremity it is connected to the hypolophid by a short bridge, a vestige of the metalophid, which isolates an elongate, sinuous anterofossettid. The mesoflexid, which is in consequence short, extends down nearly to the base of the crown. Protoconid, ectolophid and hypolophid are in a nearly straight line. The posterolophid is an isolated, somewhat slipper-shaped lamella that preserves no vestige of a former connection to



A



B

Fig. 3. *Paradelphomys fissus* gen. et sp. nov. $\times 10$. Type. Museo municipal de Mar del Plata No. 125. A, Rdm_1 — M_1 , crown view; B, Rdm_1 — M_1 , lingual view.

the hypolophid-ectolophid. The combined hypoflexid-metaflexid is a narrow, deep, parallel-sided cleft extending diagonally across the tooth. Not as deep as the mesoflexid, it is somewhat deeper on the lingual than on the labial side; at an extreme stage of wear the bases of the protoconid and hypoconid would be joined.

M₁ is square in outline anteriorly and tapers posterolingually at the crown surface, although not at the base. The anterolophid is nearly transverse anteriorly and curves posteriorly in the region of the metaconid. The mesoflexid is a diagonal slit that extends almost to the anterior extremity of the tooth and reaches downward nearly to the base of the enamel. The hypolophid-ectolophid is slightly more sinuous than in dm₄. The posterolophid is also an isolated lamella, but, unlike that of dm₄, it is decidedly convex anteriorly, the convexity marking the site of an earlier junction with the hypolophid. Posteriorly, its wall slopes outward and downward in a postero-labial direction so that its area would increase considerably with wear. The hypoflexid-metaflexid is deeper at the center than at the extremities; at an extreme stage of wear an elongate, narrow fossettid would be isolated.

Enough of the ramus is preserved to reveal that the masseteric crest began beneath the anterior end of M₁.

TABLE 1

Tooth measurements (in mm) of type specimens of
Xylechimys obliquus and *Paradelphomys fissus*

	<i>X. obliquus</i>	<i>P. fissus</i>
dm ₄ , antero-posterior	—	4.0
width, anterior	—	2.1
width, posterior	—	2.7
M ₁ , antero-posterior	3.1	3.7
width, anterior	2.5	2.9
width, posterior	2.5	2.7
M ₂ , antero-posterior	3.2	—
width, anterior	2.8	—
width, posterior	2.8	—
M ₃ , antero-posterior	2.9	—
width, anterior	2.8	—
width, posterior	2.3	—

DISCUSSION

Xylechimys invites comparison with its contemporary, *Deseadomys*. The former is more primitive as regards retention of the metalophid and anterofossettid on all molars and in the lingual extension of this lophid beyond the connection with the metaconid. It is more advanced in the greater obliquity of the hypolophid and posterolophid and in the nearly median position of the lingual end of the posterolophid. Wood and Patterson (1959:306, 309, 312) called attention to various characters of *Deseadomys arambourgi* and of *D. loomisi* that suggested close relationship, if not actual ancestry, to the Santa-Cruzean *Stichomys* and *Adelphomys*, respectively. This view still seems reasonable. *Xylechimys* does not resemble these later forms to the same extent.

Paradelphomys is decidedly specialized in the loss of the metalophid in M_1 , the very marked obliquity of the lophids and the complete separation of the posterolophid. It is, in fact, in these features the most specialized member of the Adelphomyinae so far known. There are, however, resemblances between it and *Xylechimys*, such as a nearly comparable degree of obliquity of the hypolophid and posterolophid, the lingual end of the posterolophid not extending much beyond the mid-line of the tooth until after heavy wear and the tendency toward separation of the posterolophid present in *Xylechimys*. Elimination of the metalophid, straightening of the protoconid-ectolophid-hypolophid crest, and further separation of the posterolophid would convert molars of *Xylechimys* structure into those of *Paradelphomys*. It is, of course, quite uncertain if the two stood in ancestor-descendant relationship — the more exact resemblance between the species of *Deseadomys* and *Stichomys* and *Adelphomys* would argue against this possibility — but on present evidence it seems likely that they were more closely related to each other than to any of the genera previously known.

Its name notwithstanding, *Protadelphomys* Ameghino of the Collhuehuapian is neither ancestral to *Adelphomys* nor a member of the Adelphomyinae. Ameghino (1902:112) based his concept of relationship on the lower incisors, which are relatively large, flat anteriorly, and have the transverse (mesio-distal) and antero-posterior diameters nearly equal in both. This is the only close similarity between the two forms and it is more than offset by the structure of the molars, which in *Protadelphomys* are short and quadrate rather than elongate, retain reduced metalophids on M_{1-2} , have the hypolophid directed lingually and the posterolophid deeply separated from the hypolophid. The last character is a

point of resemblance to *Paradelphomys* but it is the only one and, in view of the tendency toward lamellar structure that crops up in several of the echimyid subfamilies, we do not consider it to be indicative of any close affinity. *Protadelphomys* is known only from one incomplete ramus with broken or deeply worn teeth. What can be seen of the structure suggests that the genus represents an early and specialized offshoot of the Heteropsomyinae, and more than this cannot at present be said.

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